



## Review



## Insects–plants–pathogens: Toxicity, dependence and defense dynamics

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## ABSTRACT

In a natural ecosystem, the pathogen-plant-insect relationship has diverse implications for each other. The pathogens as well as insect-pests consume plant tissues as their feed that mostly results in damage. In turn, plant species have evolved specialized defense system to not only protect themselves but reduce the damage also. Such tripartite interactions involve toxicity, metabolic modulations, resistance etc. among all participants of interaction. These attributes result in selection pressure among participants. Coevolution of such traits reveals need to focus and unravel multiple hidden aspects of insect-plant-pathogen interactions. The definite modulations during plant responses to biotic stress and the operating defense network against herbivores are vital to research areas. Different types of plant pathogens and herbivores are tackled with various changes in plants, e.g. changes in genes expression, glucosinolate metabolism detoxification, signal transduction, cell wall modifications, Ca<sup>2+</sup> dependent signaling. It is essential to clarify which chemical in plants can work as a defense signal or weapon in plant-pathogen-herbivore interactions. In spite of increased knowledge regarding signal transduction pathways regulating growth-defense balance, much more is needed to unveil the coordination of growth rate with metabolic modulations in bi-trophic interactions. Here, we addressed plant-pathogen-insect interaction for toxicity as well as dependence along with plant defense dynamics against pathogens and insects with broad range effects at the physio-biochemical and molecular level. We have reviewed interfaces in plant-pathogen-insect research to show pulsating regulation of plant immunity for attuning survival and ecological equilibrium. An improved understanding of the systematic foundation of growth-defense stability has vital repercussions for enhancing crop yield, including insights into uncoupling of host-parasite tradeoffs for ecological and environmental sustainability.

## 1. Introduction

Other than humans and animals, microbes, insects, and land plants are dependent upon each other as the primary source of food (Howe and

Jander, 2008). Microbes and insects obtain their nourishment from living or dead plants by employing different feeding approaches (Lu et al., 2015). This food acquisition process causes injury to plant tissue (Aljibory and Chen, 2018; Mithöfer et al., 2005). In response, Plant Cells

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identify, determine, and react to Microb. Pathog., insect movements, and chemical signals. In plant-microbe-insect interactions, such chemical signatures are essential to regulate the relationship between partners at the same trophic level (Dash et al., 2017; Fürstenberg-Hägg et al., 2013; Guo et al., 2018; Howe and Jander, 2008). For instance, insect chemo-receptors determine host range suitability. Irrespective of the category i.e. whether they belong to insects or microbes, chemical signatures are vital players in selecting a plant to be used or not (Ali and Agrawal, 2012).

The capability of plants to distinguish and resist harmful microbes or insects is a specialized type of immunity. The plant immune system and its evolutionary origins have been immensely studied in plant-pathogen interactions (Ashraf et al., 2018; Hussain et al., 2018; Ifnan Khan et al., 2018; Jones and Dangl, 2006; Noman et al., 2018b, 2018c; Yi et al., 2004; Zaynab et al., 2017). The basal or primary defense against pathogens is triggered by transmembrane receptors which are responsible for recognizing PAMPs (Pathogen-Associated Molecular Patterns)/MAMPs (Microbe-associated Molecular Patterns) (Ashraf et al., 2018; Hussain et al., 2018; Noman et al., 2018b, 2018c). The PAMPs alarms the presence of invading microbes and alert for necessary actions to be taken, including transcriptional reprogramming (AbuQamar et al., 2006; An et al., 2012; Eulgem and Somssich, 2007; Islam et al., 2017, 2018a, 2018b). In the second defense layer, the resistance (R) proteins of the immune system identify pathogen effectors secreted into plant cells for tackling or weakening plant defense. Plant immune responses to pathogens mainly include the identification of PAMPs/MAMPs or, in many cases, pathogen-modified host proteins (Dang et al., 2013; Després et al., 2000; Liao et al., 2008). In plant-insect interactions, the plants use chemical defense to tackle an insect attack. In addition to phenotypic and morphological attributes, the plant uses metabolites having toxic, repellent, or anti-nutritive properties against herbivores (Fürstenberg-Hägg et al., 2013; Howe and Schaller, 2008; War et al., 2012). This is known as direct plant defense (Howe and Jander, 2008). Direct defense inhibits the growth and development of invading herbivores. Indirect plant defense includes plant volatiles and nectar induced by herbivores to attract predators (Aljibory and Chen, 2018; Appel et al., 2014; Mumm and Dicke, 2010; Noman et al., 2019). Both of these defense responses are strictly controlled. The cost of induced defense responses in plants is much lower than that of constitutive resistance (Baldwin, 1998; Lu et al., 2015). During induced resistance, plants under herbivore attack activate defense reactions at the damage site (Howe and Schaller, 2008). Moreover, physiological modulations, e.g. sugar sequestration to below-ground parts, help the plant to tolerate and fight herbivory (Lu et al., 2015; Machado et al., 2017; Schwachtje et al., 2006). Collectively, direct and indirect defenses protect the plant against a plethora of diverse herbivores in ecosystems.

The pattern of plant defense against insect attacks firmly follows the paradigm of plant immunity to microbes. Unfortunately, relatively less information is available about the molecular recognition events involved in plant immune responses against herbivores. Insect recognition systems perceive exogenous molecules like PAMPs and elicit defense response just like pathogen-triggered immunity. The elicitors can be insect-derived molecules or plant compounds altered by the insect pests (Alborn et al., 1997; Bonaventure et al., 2011; Howe and Jander, 2008). Interestingly, plants have to distinguish between simple injury and tissue damage due to insect attacks to avoid defense resource wastage (Mewis et al., 2006; Vogel et al., 2007). Activation of plant anti-microbial/herbivory defenses points out the production of endogenous signals by perturbed cells. Such signals are of critical role in perceiving danger signals. Phytohormones like jasmonates, salicylic acid (SA), and ethylene (ET), along with some other metabolites, are endogenous pervasive signals for plant tissue damage alert and succeeding defense responses to different insects (Arimura et al., 2011; Fürstenberg-Hägg et al., 2013; Guo et al., 2018; Machado et al., 2017).

It is of great interest to unravel coordinated survival strategy i.e. growth rate and metabolic modulations when plants switch to defense

mode from growth. Our information regarding plant defense (by signals, metabolites, and regulatory networks) still demands extensive investigations. We, therefore, have reviewed topical advances in the fight for survival among three important components of an ecosystem based on molecular and biochemical attributes of plant defense against microbes and herbivores. We examined, analyzed, and focused on signaling dynamics throughout microbe-plant-insect interactions and their role in plant survival. This review documents several wide-ranging effects of microbial and insect attacks at the physio-biochemical and molecular level in plant life. Finally, direct and indirect defense traits have been summarized to highlight host-plant selection and resistance.

## 2. Gene expression changes during herbivore attack

In response to biotic stress, plants experience several molecular, physiological, and biochemical changes. Notably, in case of pathogen attack or herbivory, plants undergo transcriptional modulations of linked defense genes and related metabolites. Literature about gene expression studies strongly suggests that these changes are particular. Although some overlapping induced responses have been reported during tissue damage and insect attack, however, gene expression patterns to insect attack cannot be observed during mechanical injury of plant tissue (Appel et al., 2014; Machado et al., 2017; Reymond et al., 2004b; Thompson and Goggin, 2006; Vogel et al., 2007). Therefore, we do not have two opinions about discriminated plant responses to insect herbivory only.

Advents in genomics and transcriptomics such as next-generation sequencing, RNA sequencing, and whole-genome sequence data have revolutionized the field of gene expression. Today, researchers are in a far better position than they were thirty years ago. These tools have appeared as exceptional ones for evaluating hundreds of plant genes and transcription factors (TFs) involved in different processes like defense against microbes or insect pests. Taking aid from existing reports, it is very much clear that *AtWRKY25* and *AtWRKY33* perform roles against both biotic and abiotic stresses i.e. *P. syringae* attack, salinity. During the last two decades, investigations have been carried out to study constitutive and inducible defenses in the model and non-model plants (Guo et al., 2018; Major et al., 2017; Thompson and Goggin, 2006; War et al., 2012). For instance, defense responses of *Arabidopsis thaliana*, *Brassica oleracea* and *B. nigra* were evaluated by microarrays against cabbage butterfly (*Pieris rapae* L.) and cabbage aphid (*Brevicoryne brassicae* L.) (Broekgaarden et al., 2007; Reymond et al., 2004b). Similarly, defense responses in *Triticum aestivum*, *Sorghum bicolor*, *Nicotiana attenuata* and *A. thaliana* against wheat aphid (*Schizaphis graminum* Rondani), tobacco aphid (*Myzus persicae* subsp. *nicotianae*), green peach aphid (*M. persicae* Sulzer), and grain aphid (*Sitobion avenae* Fabricius) have been well studied (Voelckel et al., 2004; War et al., 2012; Zhao et al., 2009; Zhu-Salzman et al., 2004b). Profiling of gene expression comprehensively illustrates transcriptional responses of several genes to different conditions such as abiotic stress or biotic stress. A considerable body of literature unravels elicitation of species-specific responses by one or different insects. Our analysis found evidence for considerable variation in model plant responses to different insects as enemies. Different attackers such as insects or microbes can receive different plant responses depending upon their feeding habits and the plant under attack, e.g. transcriptional modifications in *Arabidopsis* against aphid and whitefly feeding are different (Kempema et al., 2007a; Voelckel et al., 2004). Correspondingly, different plants may react differentially to the one herbivore in terms of gene expression, e.g. *P. rapae*-cabbage interaction (Broekgaarden et al., 2007). In *N. attenuata*, transcriptional responses were dissimilar for different lepidopterans (Voelckel and Baldwin, 2004). However, a comparative view of defense studies displays resembling responses of *A. thaliana* to lepidopterans' attack, i.e. cabbage butterfly (*P. rapae*) and cotton leafworm (*Spodoptera littoralis* Boisduval) (Reymond et al., 2004b). Many genes have been discovered and characterized for their involvement in plant-pathogen and plant-insect

interactions. Induction of expression of many *WRKY* genes by Microb. Pathog (Lai et al., 2008), and insect herbivory (Skibbe et al., 2008) reveals their significance in plant defense actions. For instance, *CaWRKY40* is induced by *Ralstonia solanacearum*, and its silencing compromises pepper immunity. Its overexpression in transgenic *Nicotiana benthamiana* suggests positive regulation of resistance against *R. solanacearum* attack (Dang et al., 2013). Plant resources are reallocated for defense as a consequence of gene expression variations after insect invasion. Gene expression levels are well precise measures of analyzing the transcriptional profiles variations in dissimilar genotypes of single plant species (Broekgaarden et al., 2007). Different insects are tackled with different transcriptional changes in plants. For example, changes in gene expression elicited by lepidopterans include glucosinolate metabolism, detoxification, and signal transduction. Aphids regulate genes dealing with cell wall modifications,  $Ca^{2+}$ -dependent signaling, and glucosinolate production (Reymond et al., 2004b; Thompson and Goggin, 2006). Gene expression specifically performing some roles to other attackers is a common attribute of plant defense against insect-outbreak. It has also been revealed that most of these responses reconfigure metabolism (Schwachtje and Baldwin, 2008). For instance, in *Arabidopsis*, SNF1 (Sucrose non-fermenting 1)/AMPK (AMP-activated protein kinase)/SnRK1 (SNF1-related protein kinases) play a role in detecting stress caused by insect feeding. These have a role in stress signaling as energy sensors (Crozet et al., 2014). In the same way, SnRK1 regulates photoassimilate reallocation in *N. attenuata* during herbivory. Notably, hexoses are also important for the provision of signals as well as substrates for defense responses (Tauzin and Giardina, 2014). Rodrigues and colleagues have highlighted the interesting facet of SnRK1-ABA (Abscisic acid) interaction (Rodrigues et al., 2013). Thus, it is an additional probable base of hormonal crosstalk in the interaction between plants, pathogens, and arthropods. These findings are in accordance with each other as far as plant defense is concerned. Interpretation of these outcomes verifies the presence of closely linked metabolic cues for plant protection. In *Arabidopsis*, many *cis*-elements differentiate gene regulatory frameworks taking part in defense against insect attack. The promoters of responsive genes usually possess identical elements (Appel et al., 2014; Zou et al., 2011). Hence, it seems that control of transcriptional responses against insect attacks via TFs can be a combinatorial strategy that needs several TFs to start specific expression patterns. *AtWRKYWRKY*-3 and *AtWRKY*-6 TFs are activated by *MPK3*, *MPK4*, and *MPK6*. These *WRKY* TFs are regulators of plants' responses to biotic stress. Concerning the involvement of *WRKY*-3 and *WRKY*-6 in defense against herbivory, evidence in literature ties well the defense against microbial and insect attack (Cai et al., 2015; Eulgem and Somssich, 2007; Hussain et al., 2018; Skibbe et al., 2008). Moreover, *NPR1* involvement has also been recorded in the activation of *WRKY* and *bZIP* TFs in defense against microbes in *Capsicum annum*, *N. attenuata* and *A. thaliana* (Hussain et al., 2018; Noman et al., 2017, 2018c). After activation by SA accumulation and redox changes, *NPR1* is translocated to the nucleus and functions through TFs (Pieterse and Van Loon, 2004). Correspondence amid the signal transduction elements in plants against insects and microbial attacks advocate the identical mechanisms to recognize and initiate plant responses to these organisms. In tobacco, MAP kinases, namely SIPK (SA-induced protein kinase) and WIPK (wound-induced protein kinase) are found involved in inducing responses to herbivores and wounds (Seo et al., 2007; Wu et al., 2007). *MPK6* and *MPK3* are homologs of SIPK and WIPK in *Arabidopsis*, respectively. These activate defense to counter microbial infection (Eulgem and Somssich, 2007; Takahashi et al., 2007). SIPK and WIPK also play an important role in jasmonic acid (JA) biosynthesis after elicitation of FAC (Fatty acid-amino acid conjugates) in *N. attenuata* leaves. This biosynthesis is also dependent on *NPR1* (Bonaventure et al., 2011). Our analysis of available information reveals that not a single gene or compound but a web of regulators manage defense to insect attack. The overlapping regulator activities are of substantial worth as plant safeguard. These not only endorse rapid reaction to enemies but

also decrease tissue disruption and augment chances of survival. We may attribute such a role as a credible consequence of evolution.

### 3. Defense elicitation and signal transduction in plant-microbe-insect interactions

Though gene expression is a key player in plant defense, a fundamental role is credited to the signal transduction pathways that yield a specific response (Guo et al., 2018; Zebelo and Maffei, 2014). Partially overlapping transcript patterns propose additional insect signals besides mechanical injury that activate the plant response to insects (Table 1). Such signals include chemicals linked with the insect exterior or with digestive solutions. After recognizing environmental changes in cell surroundings, a series of electric signaling events start that culminate in particular responses. In most of the plant signaling events,  $Ca^{2+}$  performs the role of second messenger inclusive of defense responses to herbivory. Under control conditions, the  $Ca^{2+}$  level in cytosol remains low as compared to organelles or apoplasmic fluid. Activation of calmodulin and some other  $Ca^{2+}$  sensing proteins, after transient increments in cytosolic  $Ca^{2+}$ , stimulate downstream signaling actions, e.g. protein phosphorylation and transcriptional activation. Maffei and co-workers demonstrated that cytosolic  $Ca^{2+}$  increased in *Phaseolus lunatus* L. under the attack of cotton leafworm (*S. littoralis*) around the site of insect bite (Maffei et al., 2006, 2007a). Conversely, after the treatment of *P. lunatus* with  $Ca^{2+}$ -chelator, neither defense genes were induced, nor volatiles were released by the feeding of plant mite (*Tetranychus urticae* Koch) (Arimura et al., 2000). It is worth discussing that IQD1-calmodulin-binding upsets the transcription of genes responsible for glucosinolate biosynthesis in *Arabidopsis* in a  $Ca^{2+}$  dependent fashion (Levy et al., 2005). Overexpressing IQD1 curtailed damages caused by a peach-potato aphid (*M. persicae*) and cabbage looper (*Trichoplusia ni* Hübner). So this allows us to confirm that IQD1 regulates plant defense responses by perceiving  $Ca^{2+}$  signals. Many important low and high molecular weight compounds, including FACs, have been observed in insect secretions (Aljibory and Chen, 2018; Bonaventure et al., 2011; Giri et al., 2006). For example, volicitin application upon wounded plants can accelerate *de novo* production and release of volatile compounds along with defense genes induction (Frey et al., 2004). The amount and composition of FACs vary among insect types. Some insects, such as tobacco budworm (*Heliothis virescens* Fabricius), seemingly decay FACs in their midgut to regulate defense inducing chemicals and emission of plant volatiles (Mori et al., 2001).

Tissue disruption by herbivores indicates the direct elicitor transfer or the indirect production of cell wall-derived elicitors capable of binding to their special receptors at the plasma membrane. Such elicitor–receptor association perturbs the outer and inner electrochemical gradient of Plant Cell. This is an important finding in the understanding of the signaling events. The mentioned perturbations may cause depolarization or hyperpolarization of *V<sub>m</sub>* and usually generate signaling cascades. Oral secretions (OSs) of insects can cause quick *V<sub>m</sub>* depolarization (Maffei et al., 2007a). Such responses have been observed in *A. thaliana*, *Ginkgo biloba*, and *Pteris vittata* (Bricchi et al., 2013; Imbiscuso et al., 2009; Mohanta et al., 2012). Mitogen-activated protein kinase (MAPK) signaling cascades also add to a growing corpus of plant biology research. Plant responses against pathogens or environmental stresses manifest strong involvement of MAPKs (Rehman et al., 2020). *LeMPK*-1, -2, and -3 play a decisive role in defense responses mediated by systemin receptors against herbivorous insects (Kandath et al., 2007; Maffei et al., 2007a). In wild rice (*Oryza minuta* J. Presl), MKK1 is induced by feeding brown planthopper (*Nilaparvata lugens* Stal) as well as the application of JA and SA (You et al., 2007). Despite the absence of an absolute MAPK pathway for insect resistance, broadly translated, our opinion indicates that these pathways are significantly involved in some plant-insect interactions (Hettenhausen et al., 2015). During the pathogen attack, pattern recognition receptors perceive PAMPs and this recognition activates MAPKs. Like PAMPs in microbes, a term was

**Table 1**

Herbivore associated elicitors (HAEs) are chemical cues produced by insect herbivores HAEs activate particular plant defense responses to fight insect pests. These structurally diverse compounds are not common elicitors of responses against insects in all plant species and normally limited to specific plant–arthropod interaction.

Plant species	HAEs						Insect species	References
	Glucose oxidase	$\beta$ -Glucosidase	N-Acyl-aminoacids	Caeliferins	Inceptin	Oligouronides		
<i>Arabidopsis thaliana</i>								Schmelz et al. (2009)
<i>Brassica oleracea</i>								Mattiacci et al. (1995)
<i>Glycine max</i>							<i>Manduca sexta</i>	(Halitschke et al., 2001; Schmelz et al., 2009)
<i>Medicago truncatula</i>							<i>Helicoverpa armigera</i>	(Bede et al., 2006; Hu et al., 2008)
<i>Nicotiana attenuate</i>							<i>Spodoptera exigua</i> <i>Drosophila melanogaster</i>	Diezel et al. (2009) (Halitschke et al., 2001; Yoshinaga et al., 2007)
<i>Nicotiana tabacum</i>							<i>Helicoverpa zea</i>	Musser et al. (2005)
<i>Phaseolus lunatus</i>							<i>Pieris brassicae</i>	(Hopke et al., 1994; Mattiacci et al., 1995)
<i>Solanum lycopersicum</i>							<i>Lepidoptera</i> and <i>Hymenoptera</i>	(Eichenseer et al., 2010; Musser et al., 2005)
							Produced by degradation of plant cell walls during insect folivory	Doares et al. (1995)
<i>Solanum melongena</i>							<i>Teleogryllus taiwanemma</i>	(Schmelz et al., 2009; Yoshinaga et al., 2007)
<i>Solanum nigrum</i>							Several <i>Lepidoptera</i>	(Pohnert et al., 1999; Yoshinaga et al., 2010)
<i>Fabaceae</i> spp.								Schmelz et al. (2009)
<i>Vigna unguiculata</i>							Produced by degradation of a plant ATP synthase during folivory by <i>Spodoptera frugiperda</i>	Schmelz et al. (2006)
<i>Zea mays</i>							<i>Spodoptera exigua</i> <i>Schistocerca americana</i>	Hopke et al. (1994) Schmelz et al. (2009) Alborn et al. (2007)

coined as herbivore-associated molecular patterns (HAMPs) for covering herbivore-based signaling molecules used to elicit defense response in plants (Mithöfer and Boland, 2012). HAMPs as elicitors trigger plant defense against insect attack after penetrating tissues during insect feeding. The first elicitor of this kind was volicitin that induces volatiles in corn to attract predators of beet armyworm (*S. exigua* Hübner) (Alborn et al., 1997). So far, FACs is the most-studied category of insect elicitors. Application of FACs to wounds can trigger particular plant responses i.e. augmented SA, JA, and ET levels along with reprogrammed transcriptome (von Dahl et al., 2007; Zebelo and Maffei, 2014). Further, FACs have been observed as elicitors for actuating MAPK signaling (Wu et al., 2007). FACs in OSs of tobacco hornworm (*Manduca sexta* L.) can enhance wound-induced expression of SA-induced MAPK. Similarly, wound-induced MAPK expression in tobacco was high (Wu et al., 2007). Additionally, compounds such as inceptin, caeliferins from fall armyworm (*S. frugiperda* J.E. Smith) and grasshopper (*Schistocerca americana* Drury) has also been noticed for their roles as elicitors in JA-, ET-mediated defense reactions against insect attack (Table 1) (Alborn et al., 2007; Schmelz et al., 2006). Results have demonstrated that volicitin, in comparison with inceptin, displayed a broad range of phytohormone-inducing activity in cultivated plants. Furthermore, inceptin-based defense induction was limited to a few plant species (Schmelz et al., 2009). This warrants a thorough investigation of insect elicitors dependent activation of plant signaling such as MAPKs and associated downstream defense actions. Keeping in mind the diverse and complex nature of plant-herbivore interactions, we anticipate the discovery of many more microbial and insect-derived elicitors taking part in triggering plant defense responses.

#### 4. Role of phytohormones in plant survival against microbial and insect attack

A crucial contributor in plant defense against pathogen attack or insect herbivory is phytohormones mediated signal transduction pathways. Phytohormones perform significant functions for plant growth, development, and survival. Different plant growth regulators have an active involvement in intra- and inter-plant communication during pathogen ingress as well as herbivores invasion (War et al., 2012). During plant defense reactions against microbes and insects, signal-transduction pathways are mediated by JA, SA, and ET (Bari and Jones, 2009; Erb et al., 2012; War et al., 2012). Depending upon the nature of the enemy, phytohormones may collaborate individually or antagonistically.

Despite the involvement of different hormones in plant defense, seminal contributions are made by jasmonates against herbivore attacks. JA triggers both direct as well as indirect defenses (Guo et al., 2018; Hatcher et al., 2004; Lu et al., 2015; Shivaji et al., 2010). JA is a derivative of linolenic acid and accrues in plant tissue upon wounding and herbivory (Zhang et al., 2008). Defense reactions induced by jasmonates are antioxidant activity, volatiles, and alkaloids (Guo et al., 2018; Lin et al., 2016, 2017; Mao et al., 2007; Pauwels et al., 2009). JA induces different genes during defense against insects (Aljory and Chen, 2018; Shivaji et al., 2010). Glucosinolate concentration is also induced by jasmonates. Prior research put forwards the interaction between jasmonates and SCFCO11 (Skip/Cullin/F-box–Coronatinsensitive 1). This enhances COI1-unit binding to jasmonate ZIM-domain proteins. This binding degrade JAZ proteins, which otherwise overpower JA-inducible expression of the gene (Sheard et al., 2010). Interaction between JAZ proteins and TFs is well able to produce a signal for modulated growth of plants under insect attack. For instance, leaf growth is negatively regulated by MYC-3,-4 TFs. JAZ proteins are repressors of MYC TFs and



work antagonistically. Degradation of JAZ proteins results in the de-repression of MYC TFs that produce a negative impact on growth (Campos et al., 2016; Major et al., 2017). Concurrent growth repression and defense induction by JAZ-MYC may offer novel strategies for enhancing the cellular defense compounds in plants under attack. Another important aspect is opposed to crosstalk between the Jasmonoyl-L-isoleucine (JA-Ile) and gibberellin (GA) signaling pathways that regulate growth-defense adjustments mediated by jasmonates. DELLA proteins inhibit GA signaling. Their involvement in the wound and jasmonate-mediated growth repression has been recorded in *A. thaliana* roots and hypocotyl but not in leaves. These results propose two points. Firstly, different growth antagonism mechanisms may maneuver in various tissues. Secondly, different DELLA family members exercise distinct influences on growth-defense antagonism through specific DELLA–JAZ interactions. Possibly by down-regulating photo-assimilation, jasmonate indirectly suppress shoot growth antagonistic to the GA pathway (Machado et al., 2017). This evidence points out that, in spite of thorough explanations about the nuclear perception of JA-Ile and related defense gene expression (Howe et al., 2018), detailed and pragmatic elucidation of growth inhibition by this hormone is needed. CDPKs (calcium-dependent protein kinases) are mediators of biotic and abiotic stress tolerance through signal transduction (Ludwig et al., 2004). JA also influences CDPK activity. In addition to the involvement of JA for direct defense against herbivores by inducing defense compounds, it is imperative in indirect defense (Barbehenn et al., 2009). JA-based EFN production is a defense measure against insects. Antioxidant enzymes (POD and PPO) are also induced by JA (Rani and Jyothsna, 2010; Shivaji et al., 2010; War et al., 2012).

Salicylic acid (SA) is an endogenous growth regulator responsible for an array of metabolic and physiological actions during plant defense, growth, and development (Aljibory and Chen, 2018; Khan et al., 2015). Both local and systemic resistances are induced by SA signaling molecules. ROS production due to the SA pathway is responsible for the induction of plant defense to insect pests, e.g. interaction of tomato and cotton bollworm (*Lycopersicon esculentum* Mill. and *Helicoverpa armigera* Hübner). Because  $H_2O_2$  is injurious for the insect digestive tract, SA-induced production of  $H_2O_2$  protects plants against pathogens and arthropod feeding (Peng et al., 2004). Very importantly, SA triggers the emission of plant volatiles to invite and entice the predators of insects (Maffei et al., 2007a). But, some studies indicate obstructed JA activity by SA and vice versa. Methyl salicylate (MeSA) is a volatile cue that activates induced plant defense, e.g. HIPV emission (De Boer et al., 2004; Maffei et al., 2007a). MeSA attracts insect predators and induces the volatiles emission to increase indirect resistance (Aljibory and Chen, 2018). But, it must be borne in mind that not all insects can induce MeSA production. For example, the damage caused by the caterpillar does not induce MeSA. Similarly, plant species also differ in their response to MeSA. Wild tobacco plants treated with MeSA did not show any attraction for predatory foragers (Diezel et al., 2009; Kessler and Baldwin, 2001). SA application on *Arabidopsis* plants also displayed non-significant results with respect to the attraction of parasitoid wasp (*Cotesia rubecula* Marshall). SA mainly induces defense to tackle piercing and sucking insects as compared to the chewing ones (Zhao et al., 2009).

As a plant growth regulator, ethylene (ET) is a vanguard against pathogenesis and herbivory. ET signaling pathway is equally important in direct and indirect plant defense against herbivores or pathogens (van Loon et al., 2006). Unlike SA, ET signaling may work synergistically or antagonistically (Kunkel and Brooks, 2002) with JA in response to pathogens and insect pests. Incremented ET levels have been limited to herbivory defense and observed in the case of mechanical wounding (Wu and Baldwin, 2010). Blocking ET perception with 1-MCP stops herbivory-induced volatiles release (Schmelz et al., 2003). This recommends ET as a key player in inducible indirect plant protection. ET usually regulates JA-mediated defense responses as compared to eliciting its defense reactions (Von Dahl and Baldwin, 2007). ET likely assists in unconstrained JA-mediated defenses against herbivores by intense SA

activity (Diezel et al., 2009). ET-JA synergistic actions elicit different plant immune responses in *L. esculentum* and *A. thaliana* (Lorenzo et al., 2003). Prior research has described 1-aminocyclopropane-1-carboxylic acid, a precursor of ET, responsible for volatile emissions from the JA treated detached leaves (Horiuchi et al., 2003). Likewise, ET additionally induced the volatiles discharge together with volicitin and JA in maize (Karban, 2011).

Plant defense is induced and regulated against pathogens and herbivores through cross-talk between phytohormones (Hussain et al., 2019). Due to the negative SA-JA cross-talk, SA pathways activation would make plants very vulnerable to enemies that are curbed through JA-dependent defense actions and vice versa. Positive or negative interactions among phytohormones support plants to reduce energy expenditures by making plant defense responses more precise to diverse attackers (Koornneef and Pieterse, 2008). Spatial and temporal separation of SA and JA can be a way out to hamper negative intervention and increase their synergistic working in indirect defense. The phytohormone controlling pathways and their influence on plants under control and stressed conditions is a complicated phenomenon. A single plant system cannot be adequate to describe the negative impacts of plant hormones activated by insect elicitors (Aqeel et al., 2019; Bamisile et al., 2018; Dash et al., 2018). Therefore, possible elicitor activated an undesirable impression of phytohormones on crop production must be recorded and compared in different systems.

## 5. Role of secondary metabolites in ameliorating insect pest attack

During the last three decades, the study of plant primary and secondary metabolites has improved our understanding of plant-plant as well as plant-other organism interactions in natural ecosystems. Studies dealing with plant metabolites are well documented. It is well acknowledged that the accumulation of plant secondary metabolites occurs as a defense strategy against pathogens, arthropods and vertebrates (DEY, 2016). The systematic facts support the view that secondary metabolites are responsible for plant defense, inclusive of resistance to specialists (Agrawal and Weber, 2015). Usually, secondary metabolites decrease herbivore performance and alter the nature of the attack on plants (Mithöfer and Boland, 2012). Several plants display a broad range of compounds with toxic effects, growth inhibition properties and feeding deterrents for insect pests (Table 2). For example, compounds (like terpenoids, alkaloids, tannins, saponins, glucosinolates) leave toxic or anti-nutritive effects on insects (Agrawal and Weber, 2015; Maag et al., 2015; War et al., 2012).

With developments in plant biology, diverse biosynthetic processes producing defense compounds have been identified. Glucosinolates are stored in plant vacuoles as inactive glucosidases (Maag et al., 2015). Thioglucosidases convert these inactive compounds, in case of infestation, into thiocyanates, isothiocyanates, nitriles, or epithionitriles (Halkier and Gershenzon, 2006). Recent studies have confirmed the role of glucosinolates in defense-related signaling. For instance, the production and breakdown of 4-methoxyindol-3-ylglucosinolate (4MI3G) are needed to induce callose deposition due to the flg22 effect in *A. thaliana* (Clay et al., 2009). 4MI3G deficient mutant lines failed to accumulate callose. Less callose deposition enhances infection and reduces the resistance of plants against green peach aphid and microbial pathogens, e.g. powdery mildew (*Blumeria graminis hordei*, *Erysiphe pisi*) (Bednarek et al., 2009; Pfalz et al., 2009). Ahmad et al. (2011) have suggested an important role of benzoxazinoids in internal defense signaling against microbes. Maize lines with impaired benzoxazinoid biosynthetic pathway did not show any chitosan-triggered deposition of callose and became sensitive to corn fungal pathogen (*Setosphaeria turcica* Luttrell) (Ahmad et al., 2011). Exogenously applied DIMBOA-glucoside (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one), a toxin, restored callose deposition in mentioned maize line. Interestingly, DIMBOA also mediates defense against corn leaf aphid (*Rhopalosiphum*

**Table 2**

Many naturally occurring compounds are capable of performing insecticidal activity that is protection tactics for plants. The compounds such as proteins or lectins possess anti-nutritive/toxic properties. Toxic proteins are absorbed in digestive tract and reach hemolymph, then leads to insect death. Some of these substances like SOD, POD, PI, LOX may function enzymatically or lectins bind to other compounds in gut causing injurious effects (Chakraborti et al., 2009; Chen et al., 2005; 2007; De Leo et al., 2001; Dunse et al., 2010; Dutta et al., 2005; Fidantsef et al., 1999; Giovanini et al., 2007; Heng-Moss et al., 2004; Hui et al., 2003; Kant et al., 2004; Kempema et al., 2007b; Kuśnierczyk et al., 2007; Macedo et al., 2007; Mercke et al., 2004; Moran et al., 2002; Ralph et al., 2006; Reymond et al., 2004a; Reymond et al., 2000; Ruther and Kleier, 2005; Saha et al., 2006; Schmidt et al., 2005; Sethi et al., 2009; Stoger et al., 1999; Stout et al., 2009; Sun et al., 2002; Vandendorre et al., 2009; Wei et al., 2007; Zhu-Salzman et al., 2004a).

Plant species	Defense Compounds															Role		Role against	References							
	Proteins involved in defense										Lectin & Lectin like proteins					Antinutritional	Toxic									
	Proteinase inhibitors	Lipoxy genases	Pero xidases	polyphenol oxidases	Hevein-like protein	Catalase	superoxide dismutase	Arginase	Asc oxidase	Oxalate oxidase	Thr deaminase	Chitinases	Cys proteases	Hevein-like protein	Leuamino peptidase					Lectins	Allium sativum leaf lectin	Jacalin-like lectins	Snowdrop lectin	Nicotiana-related lectins		
<i>Alnus glutinosa</i>																					√		<i>Agelastica alni</i>	(Sethi et al., 2009)		
<i>Arabidopsis</i>																						√		<i>A. alni</i>	(Sethi et al., 2009)	
																						√		<i>Bemisia tabaci</i>	(Kempema et al., 2007b)	
																						√		<i>B. tabaci</i>	(Kempema et al., 2007b)	
																						√		<i>Myzus persicae</i>	(Kuśnierczyk et al., 2007)	
																						√		<i>Brevicoryne brassicae</i>	(Kuśnierczyk et al., 2007)	
																							√		<i>Pieris rapae</i>	(Reymond et al., 2004a)
																							√		<i>Spodoptera littoralis</i>	(Reymond et al., 2004a)
																							√		<i>P. rapae</i>	(Reymond et al., 2000)
																							√		<i>B. tabaci</i>	(Kempema et al., 2007b)
																							√		<i>M. persicae</i>	(Moran et al., 2002)
																							√		<i>Pieris rapae</i>	(Reymond et al., 2004a)
																							√		<i>Spodoptera littoralis</i>	(Reymond et al., 2004a)
	<i>Transgenic Arabidopsis / Tobacco</i>																						√		<i>S. littoralis</i>	(Stoger et al., 1999)
																						√		<i>Pieris rapae</i>	(Reymond et al., 2004a)	
																						√		<i>S. littoralis</i>	(Reymond et al., 2004a)	
																						√		<i>S. exigua</i>	(De Leo et al., 2001)	
<i>Transgenic Arabidopsis /Oil seed rape</i>																						√		<i>Plutella xylostella</i>	(De Leo et al., 2001)	
																						√		<i>Mamestra brassicae</i>	(De Leo et al., 2001)	
<i>Bouteloua dactyloides</i>																						√		<i>S. littoralis</i>	(De Leo et al., 2001)	
																						√		<i>S. exigua</i>	(De Leo et al., 2001)	
<i>Cicer arietinum</i>																						√		<i>Blissus oxidius</i>	(Heng-Moss et al., 2004)	
																						√		<i>B. oxidius</i>	(Heng-Moss et al., 2004)	
<i>Zea mays</i>																						√		<i>Aphis craccivora</i>	(Dutta et al., 2005)	
																						√		<i>S. littoralis</i>	(Ruther and Kleier, 2005)	
<i>Cucumis sativus</i>																						√		<i>S. littoralis</i>	(Reymond et al., 2004a)	
																						√		<i>Tetranychus urticae</i>	(Mercke et al., 2004)	
<i>Gossypium hirsutum</i>																						√		<i>Helicoverpa armigera</i>	(Dunse et al., 2010)	
																						√		<i>Lymantria dispar</i>	(Wei et al., 2007)	
<i>Hybrid poplar</i>																						√		<i>Malacosoma disstria</i>	(Ralph et al., 2006)	
																						√		<i>M. disstria</i>	(Ralph et al., 2006)	
<i>Medicago sativa</i>																						√		<i>Aphis medicaginis</i>	(Wei et al., 2007)	
																						√		<i>A. medicaginis</i>	(Wei et al., 2007)	

<i>Nicotiana attenuata</i>	■																		√	<i>Spodoptera littoralis</i>	(Hui et al., 2003)	
		■																	√	<i>Bemisia tabaci</i>	(Kempema et al., 2007b)	
																			√	<i>Myzus nicotianae</i>	(Voelckel et al., 2004)	
																			√	<i>Manduca sexta</i>	(Schmidt et al., 2005)	
<i>Oryza sativa</i>																			√	<i>M. sexta</i>	(Schmidt et al., 2005)	
																			√	<i>Spodoptera frugiperda</i>	(Stout et al., 2009)	
<i>Solanum nigrum</i>																					(Sun et al., 2002)	
																			√	<i>M. sexta</i>	(Ralph et al., 2006)	
<i>Sorghum bicolor</i>																			√	<i>M. sexta</i>	(Schmidt et al., 2005)	
																			√	<i>Schizaphis graminum</i>	(Zhu-Salzman et al., 2004a)	
<i>Nicotiana tabacum</i>																			√	<i>S. graminum</i>	(Zhu-Salzman et al., 2004a)	
																				Aphids	(Chakraborti et al., 2009)	
																				<i>Anagasta kuehniella</i>	(Macedo et al., 2007)	
																				<i>Spodoptera littoralis</i>	(Vandenborre et al., 2009)	
<i>Solanum lycopersicum</i>																				√	<i>M. sexta</i>	(Vandenborre et al., 2009)
																				√	<i>M. sexta</i>	(Chen et al., 2007; Chen et al., 2005)
																				√	<i>Macrosiphium euphorbiae</i>	(Fidantsef et al., 1999)
																				√	<i>Myzus persicae</i>	(Fidantsef et al., 1999)
																				√	<i>M. sexta</i>	(Chen et al., 2005)
																				√	<i>Spodoptera frugiperda</i>	(Bhonwong et al., 2009)
																				√	<i>Helicoverpa armigera</i>	(Bhonwong et al., 2009)
																				√	<i>M. sexta</i>	(Chen et al., 2005)
																				√	<i>M. sexta</i>	(Chen et al., 2007)
																				√	<i>M. sexta</i>	(Hui et al., 2003)
																				√	<i>Trichoplusia ni</i>	(Chen et al., 2007; Chen et al., 2005)
	<i>Triticum aestivum</i>																				√	<i>Tetranychus urticae</i>
																				√	<i>T. urticae</i>	(Kant et al., 2004)
																				√	<i>M. sexta</i>	(Chen et al., 2007)
																				√	<i>Sitobion avenae</i>	(Zhao et al., 2009)
																					(Giovannini et al., 2007)	
																					<i>Nilaparvata lugens</i>	(Saha et al., 2006)

*maidis* Fitch) (Meihls et al., 2013). Together, these results confirm that DIMBOA-glucoside may function in resistance to aphids as glucosinolates do by signaling for increased callose deposition. Nevertheless, we can have an opinion that activated glycoside defense armaments after tissue injury are capable of working as intra-plant signals and regulators of the immune responses.

More than 9000 phenolic compounds have been recorded in plants. Different illustrations of positive interactions between root herbivore and phenolic concentrations are on record (Johnson and Nielsen, 2012). Phenols are usually involved in defense mechanisms against microorganisms, herbivores, and competing plant species. For instance, lignin has a role in plant resistance to pathogens as well as insects (War et al., 2012). The results provide evidence for lignin-mediated restriction on pathogens entry by blocking or enhancing the leaf hardness to avoid herbivores feeding (Barakat et al., 2010). It may also reduce the leaf's nutritional status. This argument follows that herbivory or pathogenesis can induce lignin synthesis, and its quick deposition hampers pathogen or herbivore growth and spread (Johnson et al., 2009). After plant infestation with pests and pathogens, elevated expression of lignin associated genes e.g. CAD/CAD-like genes is also on record (Barakat et al., 2010). Phenol oxidation by PPO and POD is the primary defense component in plants against abiotic and biotic stresses (Noman et al., 2018a; Noman and Aqeel, 2017; War et al., 2012). The significant responsibility shared by proteins in the immunity process highlights that secondary metabolites are the main determining factor of host utilization by insects (Table 2). Quinones, a product of phenols oxidation, cause direct toxicity to insect pests. It covalently attaches to leaf proteins for stopping protein digestion in insects. Similarly, amino acids alkylation decreases the nutritional worth of plant proteins for insects that badly influence their growth and development (Bhonwong et al., 2009).

Phenols also cause cyclic reduction of ROS and H<sub>2</sub>O<sub>2</sub> to prevent oxidative damage and activate defense enzymes (Maffei et al., 2007b). Simple phenolics, i.e. salicylates, act as antifeedant to winter moth (*Operophtera brumata* L.). Salicylate levels and larval growth are also correlated negatively. But, SA is valuable as a plant growth regulator rather than a deterrent (Simmonds, 2003).

Flavonoids are polyphenolic compounds with C6–C3–C6 backbone (Cheynier et al., 2013). The role of flavonoids in plants as anti-herbivory guards has been well described in different studies. Results provide a basis for the high mortality of *S. frugiperda* larvae reared on flavonoid, i.e. quercetin-rich artificial diet (Hafeez et al., 2020). Probably, quercetin blocked the mitochondrial ATPase and constrained the detoxification process in the insect gut (Gallo et al., 2006; Yu and Abo-Elghar, 2000). Such findings also add to a growing corpus of research showing that flavonoids are also involved in several signaling processes other than defense e.g. auxin signaling (Cheynier et al., 2013; Peer and Murphy, 2007). Remarkably, flavonoids play a role in establishing the symbiotic relationship between plant and microbe e.g. nodule formation (Gibson et al., 2008). Besides, due to their role as feeding deterrents, tannins are very injurious for phytophagous insects. These bind to the insect proteins, reduce their nutritional status, and results in midgut wounds (Barbehenn and Constabel, 2011; Sharma et al., 2009). Tannins precipitate proteins nonspecifically, chelate metal ions, and lessen their bioavailability for insects. It has been reported that tannins play a significant role in plant resistance to different stresses and induce specialized response against insect damage (Barbehenn and Constabel, 2011). Tannins in response to gypsy moth (*Lymantria dispar* L.), brown-tail moth (*Euproctis chryssorrhoea* L.) and winter moth (*O. brumata*) function as feeding deterrents (Bernays, 1981). Likewise, in groundnut, polymers of procyanidin act as feeding deterrent against

cowpea aphid (*Aphis craccivora* Koch). The transcriptional trigger of the flavonoid pathway can induct tannins in *Populus* leaves against wounding and insect herbivory. But, some polyphagous insects like desert locust (*Schistocerca gregaria* Forskål) possess the capacity to endure gallotannins. The functional diversity of plant metabolites and the evolution of insect counter-defense strategies are proof of the battle for survival between plants and insect pests. The discussed information stresses that plant secondary metabolites' actions must be explored in a highly cohesive and universal view.

#### 6. Plant's volatile arsenal during the defense

Volatiles emission during insect attack (HIPV, Herbivore-induced plant volatiles) offers direct and indirect defense assistance by deterring insects or attracting their predators (Kessler and Baldwin, 2001; Lin et al., 2017). This love and hate phenomenon due to volatile release has been well investigated in different plants (Voelckel et al., 2004; War et al., 2012). The HIPVs arbitrate the interfaces among plants-insects, -microbes, -neighboring plants (Lin et al., 2016). Among their prominent functions, HIPVs are progressively involved as aerial alerts that advise undamaged plant parts regarding insect attacks and activate the need for prior defense. This aspect suggests that emission of volatile blends from damaged leaves instigate nearby leaves to increment their direct chemical defenses against enemies as well as elevate the extra-floral nectar secretion to attract predators (Frost et al., 2007; Heil and Bueno, 2007). Parasitoids trace their prey with the help of plant-derived odors that is, in fact, a defense strategy of volatiles emitting plants. *AtTPS10* is a herbivory induced gene responsible for the production of sesquiterpenes like (*E*)- $\beta$ -farnesene, (*E*)- $\alpha$ -bergamotene (Schnee et al., 2006). Parasitoid-prey interaction between parasitoid wasp (*C. marginiventris* Cresson) and cotton leafworm (*S. littoralis*) displayed subsequent attraction to TPS10-producing *A. thaliana* because the wild type is unable to produce a considerable quantity of terpenes. So, we can infer that induction of a single herbivore-associated gene can be adequate for eliciting indirect plant defense. Production of HIPVs varies with type, developmental stage, condition of plant and insect type as well. The volatile blend produced against insect attack is specific for a particular insect-plant system (Arimura et al., 2009; Maffei, 2010).

A critical appraisal of HIPVs reveals green leaf volatiles (GLVs), the reactive electrophile species having a role in stress tolerance, are the well-studied members of this defense arsenal. GLVs have a crucial role in plant defense by attracting natural enemies of insects (Arimura et al., 2009; War et al., 2011, 2012). Sometimes, volatile signals do not result in quick defenses instead prepare a plant part to retort with a quicker and durable defense. In herbivore attacked maize plants with induced volatile blends, fumigation of poplar and GLVs, results in the formation of proteinase inhibitors, the anti-herbivore defense enzyme (Frost et al., 2008; Karban et al., 2006; Ton et al., 2007). HIPVs (like MeSA) also attract predators i.e. mites, green lacewing, ladybird beetle (De Boer et al., 2004; James, 2003). The oviposition of the cabbage moth (*Mamestra brassicae* L.) is inhibited by MeSA during the infestation. In the light of a report by Ulland et al. (2007), we confirm that attacking herbivores can also detect MeSA. In insect-infested plants, Methyl benzoate (MeBA) activity has also been recorded (Chen et al., 2003). Here, another important aspect to be kept in mind is the ecological cost of using HIPVs. HIPVs are also able to attract crop pests. Colorado potato beetle (*Leptinotarsa decemlineata* Say) is attracted to the volatile blend of cis-3-hexenyl acetate, linalool, and MeSA (Dickens, 2006). Metabolites, products yielded in lipoxygenase (LOX), Shikimic acid and terpenoid pathway perform critical functions in direct and indirect plant defense (Gill et al., 2010). Blend of mono-, sesqui- and homoterpenes have been noticed in black cottonwood (*Populus trichocarpa* Torr. & Gray) after the attack of gypsy moth (*L. dispar*). (Z)-3-hexanol treated maize plants induced emission of volatile blend that is generally emitted after caterpillar attack for attracting the natural enemies. Volatiles don't need to be produced by above-ground plant parts. These can be

produced and released below the soil. For example, (*E*)- $\beta$ -caryophyllene released by corn (*Zea mays*) roots attracts *Heterorhabditis megidis* nematodes that are the natural enemy of beetle larvae. (*E*)- $\beta$ -caryophyllene treated plants attracted *H. magidis* and decreased herbivory (Rasmann et al., 2005). Hence, the roles of HIPVs are precise and essential for plant species interacting with insect herbivores. Studies focusing on evolution, biosynthesis and spread and activity levels of volatiles in different plant species will cast light upon the processes of distinguishing attackers.

#### 7. Conclusion

We conclude that adjusting and managing growth and survival balance among plants-herbivores and pathogens involve extensive physio-biochemical modulations and tradeoffs. It is not solely important to save plant and leave other contributors in interaction. Genetic adaptations for survival among studied participants need much attention for broader perspective of relationship. Exploiting the defense genes expression can be more effective by making use of resistance mechanism with abridged deleterious pleiotropic influences on growth and productivity. Prospective efforts to characterize metabolites as defense weapons or signals would prove quite beneficial. Answering research questions related to feedback loops, links to downstream transcriptional and metabolic vicissitudes also demand immense attention. Increments in data on defenses as well as defense signals could enhance the understanding of the compounds with dual functions. The concept of coordinated control of disease/herbivory must be given appropriate weightage rather than considering all as enemies and mutualistic interactions must not be ignored. We suggest making of a model based upon ecological and physio-biochemical attributes for understanding the issue and its management. Additionally, pathogen-insect-plant interactions must be immensely focused for exploring specificities of this relationship and understanding their coevolution. It is need of the hour to develop ground breaking techniques to stop the worldwide damage to crops caused by insect-borne pathogens.

#### Declaration of competing interest

The authors declared that there are no known conflicts of interest associated with this manuscript.

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#### List of Abbreviations

ABA	(Abscisic acid)
AMPK	(AMP-activated protein kinase)
bZIP	(Basic Leucine Zipper)
Ca <sup>2+</sup> dependent	(Calcium dependent)
CAD	(Carbamoyl-phosphate Synthetase 2, Aspartate Transcarbamoylase, & Dihydroorotase)
CDPKs	(calcium-dependent protein kinases)
DIMBOA	(2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one)
EFN	(Extrafloral nectar)
ET	(Ethylene)
FAC	(Fatty acid-amino acid conjugates)
GA	(Gibberellin)
GLVs	(Green leaf volatiles)
H <sub>2</sub> O <sub>2</sub>	(Hydrogen peroxide)
HAMPs	(Herbivore-associated molecular patterns)
HIPV	(Herbivore-induced plant volatiles)
IQD1	(IQ domain1)
JA	(Jasmonic acid)



JA-Ile	(Jasmonoyl-L-isoleucine)
JAZ	(Jasmonate ZIM-domain)
LeMPK	( <i>Lycopersicon esculentum</i> mitogen-activated protein kinase)
LOX	(Lipoxygenase)
MAMPs	(Microbe-associated Molecular Patterns)
MeSA	(Methyl salicylates)
NPR1	(Nonexpressor of pathogenesis-related genes 1)
OSs	(Oral secretions)
PAMPs	(Pathogen-Associated Molecular Patterns)
POD	(Peroxidase)
PPO	(Polyphenol oxidase)
ROS	(Reactive oxygen species)
SA	(Salicylic acid)
SCFCOII	(Skip/Cullin/F-box– Coronatin-Insensitive 1)
SIPK	(SA-induced protein kinase)
SNF1	(Sucrose non-fermenting 1)
SnRK1	(SNF1-related protein kinases)
TFs	(Transcription factors)
TPS	(Terpene synthases)
Vm	(Plasma membrane potential)
WIPK	(wound-induced protein kinase)
ZIM	(Zinc-finger inflorescence meristem)
MKK	(Mitogen-activated protein kinase kinase)
MPK	(Mitogen-activated protein kinase)

### Credit author statement

Ali Noman: Conceptualization, Ali Noman, Muhammad Aqeel: Data curation, Writing – original draft, Validation, Noreen Khalid, Noreen Akhtar: Visualization, Investigation, Waqar Islam, Ghulam Yasin, Muhammad Qasim, Saad Alamri, Omar Mahmoud AlZoubi and Abdullah Al-sadi: Resources, Writing- Reviewing and Editing, Mohamed Hashem: Funding acquisition.

### Ethical statement

This article does not contain any studies with human or animal subjects. We declare that we do not have conflict of interest.

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